Fledging size and survival in snow geese: timing is everything (or is it?)

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ABSTRACT   *In many birds, body size at fledging is assumed to predict accurately the probability of subsequent survival, and size at fledging is often used as a proxy variable in analyses attempting to assess the pattern of natural selection on body size. However, in some species, size at fledging can vary significantly as a function of variation in the environmental component of growth. Such developmental plasticity has been demonstrated in several species of Arctic-breeding geese. In many cases, slower growth and reduced size at fledging has been suggested as the most parsimonious explanation for reduced post-fledging survival in goslings reared under poor environmental conditions. However, simply quantifying a relationship between mean size at fledging and mean survival rate (Francis et al., 1992) may obscure the pattern of selection on the interaction of the genetic and environmental components of growth. The hypothesis that selection operates on the environmental component of body size at fledging, rather than the genetic component of size per se, was tested using data from the long-term study of Lesser Snow Geese (Anser c. caerulescens) breeding at La Pérouse Bay, Manitoba, Canada. Using data from female goslings measured at fledging, post-fledging survival rates were estimated using combined live encounter and dead recovery data (Burnham, 1993). To control for the covariation between growth and environmental factors, survival rates were constrained to be functions of individual covariation of size at fledging, and various measures of the timing of hatch; in all Arctic-breeding geese studied to date, late hatching goslings grow significantly more slowly than do early hatching goslings. The slower growth of late-hatching goslings has been demonstrated to reflect systematic changes in the environmental component of growth, and thus controlling for hatch date controls for a significant proportion of variation in the environmental component of growth. The relationship between size at fledging, hatch date and survival was found to be significantly non-linear; among early hatching goslings, there was little indication of significant differences in survival rate among large and small goslings. However, with increasingly later hatch*

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dates, there was progressively greater mortality selection against smaller, slower growing goslings in most years. This would appear to suggest that body size matters, but not absolutely; small size leads to reduced survival for late-hatching goslings only at La Pérouse Bay. Since at least some of the variation in size among goslings for a given hatch date reflects genetic differences, this suggests selection may favour larger size at fledging, albeit only among late-hatching goslings.

1 Introduction

The ecological and evolutionary implications of body size have been extensively studied by biologists, in part because of the relative ease with which body size can be measured. In many species, body size influences social status, fecundity and survival. Thus, understanding the evolution of size is potentially important to the understanding of the population biology of a particular species.

Endler (1986) defines selection as a process such that if a population has variation among individuals in one or more traits affecting fitness, and if this variation is to some degree genetically heritable, then the distribution of these traits may change in predictable ways over generations (see also Manly, 1990; Roff, 1997). Further, since adaptive evolution requires that variation in fitness associated with phenotypic variation be at least under partial genetic control, differences in fitness associated with environmental variation may be evolutionarily neutral (although predicting the effects of selection on norms of reaction can be complex; Stearns, 1992).

While methods exist for quantitative analysis of selection on infinite-dimensional characters such as growth and size (Kirkpatrick, 1988; Lynch & Arnold, 1988), partitioning selection between the genotypic and environmental components of size or growth rate is often difficult. This is especially true in populations studied under natural conditions, where there is often little known about the underlying genetics affecting body size and little if any 'experimental' control over the environmental conditions under which those genetics are expressed.

In the absence of experimental data, one approach is to consider differences in correlations in measures of body size between the parents and offspring as reflecting environmental and not genetic variation (van Noordwijk *et al.*, 1988; Alatalo *et al.*, 1990). In such an analysis, negative residuals from a parent-offspring regression might indicate slower growth due to poor environmental conditions experienced by the offspring during early growth and development. However, when applied to traits such as growth rate or size, these approaches often assume that parental size is itself not permanently influenced by environmental conditions. Nonetheless, in some cases it is possible to demonstrate unequivocally that a significant proportion of the phenotypic variation in growth rate or body size reflects primarily differences in the environmental component.

Such environmental variation in the expression of several phenotypic traits has been particularly well documented in several studies of herbivorous Arctic-breeding geese. In particular, significant phenotypic plasticity of body size related to environmental conditions experienced during early development is virtually ubiquitous in both adult and juvenile geese (Cooch *et al.*, 1991a,b, 1993; Sedinger & Flint, 1991; Larsson & Forslund, 1992; Lindholm *et al.*, 1994; Sedinger *et al.*, 1995; Larsson *et al.*, 1998). As an adaptation to the short Arctic breeding season, goslings of Arctic-breeding geese exhibit extremely rapid growth for a species with precocial young (tabulated in Whitehead *et al.*, 1990). As a result, growth and development

of goslings is highly sensitive to variation in the quality and quantity of food, which in turn is strongly influenced by the geese themselves. For example, at La Pérouse Bay, grazing pressure over the course of the breeding season reduces both above-ground forage and the capacity of salt-marsh vegetation to show compensatory growth following grazing (e.g. Hik & Jefferies, 1990). This intraseasonal pattern of variation in food abundance and quality has a profound impact on growth and early survival of goslings. In general, late-hatching goslings are both structurally smaller and lighter for a given age than earlier hatching goslings (Cooch *et al.*, 1991a; Sedinger & Flint, 1991; Larrson & Forslund, 1992; Lindholm *et al.*, 1994; Lepage *et al.*, 1999), and show lower rates of recruitment (i.e. survival) than early hatching goslings (Cooke *et al.*, 1984, 1995). Such seasonal variation in gosling growth and survival has been clearly demonstrated to reflect variation in the environmental, and not the genetic, component of gosling growth (Cooch *et al.*, 1991a; Sedinger *et al.*, 1997).

In this study, I used data from a long-term study of a population of the lesser snow goose (*Anser C. caerulescens*; hereafter, snow goose) breeding at La Pérouse Bay, Manitoba, Canada, to address the general question of the relationship between gosling size at fledging, and subsequent survival. In particular, I attempted to assess the degree to which selection may be operating on either the genetic or environmental component of gosling size, by controlling for sources of environmental variation in gosling growth and development. Significant size-dependent differences in gosling survival when the primary sources of environmental variation are controlled for would be consistent with the hypothesis that selection is operating on the genetic component of gosling size.

1.1 The larger context—environmental change at La Pérouse Bay

Although the sensitivity of gosling size at fledging to variation in conditions experienced during growth has been well established for Arctic-nesting geese in general, analysis of gosling growth data from La Pérouse Bay is complicated by systematic environmental changes over years. These changes have been precipitated by significant increases in the size of the La Pérouse Bay nesting population, from approximately 2000 nesting pairs in 1968 to present estimates of 25 000- 35 000 nesting pairs (Cooke *et al.*, 1995). High intensity grazing and (particularly) early-season grubbing by increased numbers of geese have reduced the standing crop of food available at La Pérouse Bay (Hik & Jefferies, 1990; Hik *et al.*, 1991; Williams *et al.*, 1993). This has precipitated a trophic cascade that has reduced both the capacity of the forage plants to recover from grazing, and the standing crop of available forage (Bazely & Jefferies, 1996; Abraham & Jefferies, 1997; Jefferies, 1997, 1999). Over the course of the study, approximately 70% of the salt-marsh graminoid swards have been severely damaged, approaching 100% in some of the most heavily used traditional nesting and foraging areas at La Pérouse Bay (Cooch *et al.*, 2001).

This reduction in available food over years has led to a significant long-term decline in growth of goslings, and a decline in size among those birds surviving to adulthood (i.e. little to no compensatory growth between fledging and adulthood; Cooch *et al.*, 1991b). As with the general pattern of seasonal variation in gosling growth, Cooch *et al.* (1991b) showed that these annual changes reflected a systematic change in the *environmental* component of body size, and not a change in the underlying *genetic* structure of the population.

Concurrent with these long-term changes, gosling survival has declined over time, both during the pre-fledging period (i.e. between hatch and fledging; Williams *et al.*, 1993), and during the year after fledging (Francis *et al.*, 1992). In both cases, the declines in gosling survival were suggested to reflect systematic decreases in gosling growth and body condition. Francis *et al.* (1992) showed that there was a positive correlation between annual mean gosling size (mass) and annual post-fledging gosling survival rate estimated from data from dead recoveries. They argued that the long-term decline in gosling recovery rate indicated that much of the decrease in survival likely occurred before the goslings migrated south from the breeding colony; since a gosling must fly south from the colony (i.e. survive long enough to be capable of flight) in order to be shot and recovered (see also Cooke & Francis, 1993; Cooch *et al.*, 1993).

1.2 *Gosling survival and body size—genetics or environment?*

Results from these previous studies would appear to indicate that much of the variation in gosling survival reflects differences in the environmental component of body size. A preliminary analysis by Cooke *et al.* (1995) found some evidence to suggest that body size did significantly influence post-fledging survival of goslings, but only among goslings that hatched late relative to other goslings in a given season; larger late-hatched goslings had higher post-fledging survival than did smaller late-hatched goslings. They suggested that among early-hatched goslings, there was no relationship between gosling size and survival. Because the slower growth of late-hatching goslings has been shown to reflect systematic seasonal changes in the environmental component of gosling growth, rather than genetic variation (Cooch *et al.*, 1991a; Sedinger *et al.*, 1997), Cooke *et al.* (1995) suggested that gosling size at fledging was selectively neutral.

However, this preliminary analysis was limited, in several respects. First, in their analysis, Cooke *et al.* assessed variation in survival between discrete body size classes (large and small), rather than as a function of size expressed as a continuous covariate. Although partitioning body size into a large number of groups typically yields equivalent results, doing so reduces the statistical efficiency of the analysis, and does not allow for easy detection of non-linear relationships between size and survival (as would be expected under normalizing selection on body size).

Second, their analysis was conditioned on classification of hatch date as 'early' or 'late' *relative* to other nests in a given season. The analysis presented by Cooke *et al.* did not account for the significant annual differences in *absolute* mean hatch date at La Pérouse Bay. Francis *et al.* (1992) showed that first-year survival of goslings hatched in late years was significantly lower than survival of goslings hatched in earlier years, corresponding to lower overall gosling size in late years (Cooch *et al.*, 1991b). In late years, goslings are typically too small to fly before the onset of winter. Thus, it might be reasonable to predict that mortality of smaller, slower growing goslings might be most acute among late hatching goslings in late years.

Finally, the interpretation of Cooke *et al.* (1995) that gosling body size may be selectively neutral was based on the assumption that size variation among early-hatching goslings (where no size-specific differences in survival were detected) reflected primarily genetic variation, while variation in growth among late-hatching goslings (where larger goslings had higher probabilities of survival than smaller goslings) reflected environmental variation. However, seasonal and annual variation

in gosling size is perhaps best considered as a norm of reaction (Stearns, 1992); the variation in size of late-hatching goslings reflects a particular interaction of the various genotypes for body size (which are probably reasonably assumed to be random with respect to hatch date) with the environment. What is unknown is whether large late-hatching goslings are also genetically larger; parent-offspring comparisons are non-informative in this study because of the significant plasticity in adult size (Cooch *et al.*, 1991b). Characterization of the norm of reaction would require having one or more genetic markers for gosling growth.

In this study, I reassess the relationship between gosling size at fledging and variation in post-fledging survival. I specifically control for various sources of variation in the environmental component of gosling size, in an attempt to assess as directly as possible under natural conditions the degree to which mortality selection may be operating on gosling size.

2 Methods

Data on the breeding biology of the Snow Goose have been collected annually from the colony at La Pérouse Bay (LPB) from 1968 to the present. General field methods are described elsewhere (Cooke *et al.*, 1995). Those particular procedures relevant to this study are described briefly here.

The colony, presently numbering 15 000- 20 000 breeding pairs, is located on the southern edge of the species' breeding range. Each year, ca. 2000 nests were monitored at hatching, and each hatchling was weighed and marked with an individually numbered web-tag. Approximately five weeks after hatch, before the goslings are fully fledged, the adults moult their primary flight feathers and are temporarily flightless. By this time, non-breeders have left the colony for distant moulting sites (i.e. adults captured during ringing have at least attempted to breed). While the adults are flightless, ca. 1500 families (ca. 4000- 5500 adults and goslings) were rounded up, aged, sexed, and ringed. A proportion of goslings and adults captured each year were also measured and weighed.

2.1 Body size measurements and adjustments

I compared first-year survival among female goslings using body mass (measured to the nearest gram) as an index of 'body size'. Although multivariate measures are generally preferred in analyses of structural size (Rising & Somers, 1989), I used body mass as an index to 'body size' for two reasons. First, it was measured for the largest number of goslings in the data set. Second, body mass reflects contributions of both structural size and condition, each of which may contribute to the probability of survival. Hereafter, I refer to variation in body mass only.

Gosling body mass at fledging varies as a function of several factors. Clearly, body mass will increase with age to some point. Previous analysis of data from this population has indicated that, over the range of ages at which goslings are captured at ringing (25- 40 days), growth is effectively linear (such that variation in body size and growth rate are equivalent; Cooch *et al.*, 1997, 1999). To control for age-specific variation in mass, I analysed residuals of a simple linear regression of body mass (g) on age (in days) at ringing (when the goslings were measured). There was no trend in either the absolute mean or variance of the residuals with age at banding.

2.2 Timing—absolute versus relative hatch date

In this study, I used hatch date as a proxy for 'environmental conditions'; in general, the later the hatch date, the poorer the quality and quantity of food plants (Hik *et al.*, 1991; Lepage *et al.*, 1999), and the slower the growth of goslings (Cooch *et al.*, 1991a; Sedinger & Flint, 1991; Larsson & Forslund, 1992; Lepage *et al.*, 1999). While other environmental factors may contribute significantly to variation in gosling growth (e.g. weather; Cooch *et al.*, 1991b), the effects of timing of hatch, and the relationship between hatch date and food, contribute the greatest proportion of the environmental variation in gosling growth (Cooch *et al.*, 1991a,b).

The effects of hatch date on gosling growth and first-year survival need to be considered in terms of both *absolute* and *relative* time scales. Absolute annual mean hatch dates at La Pérouse Bay have varied significantly among years, ranging from as early as 15 May (1980) to as late as 17 June (1983) (Fig. 1). To test for differences in survival as a function of variation in absolute hatch date, I classified each year in the data set as either 'early', 'average' or 'late'. I used these ranks as either (i) levels of a classification variable (for tests of general heterogeneity as a function of absolute hatch date), or (ii) coded as a linear covariate (which explicitly reflects the ordinal nature of the predicted decrease in survival with later hatch date).

To account for differences in survival as a function of relative hatch date, individuals were grouped according to relative hatch date coded as either 'early' ($<$ mean annual hatch date $- 0.45 \times$ SD), 'average' or 'late' ($>$ mean annual hatch
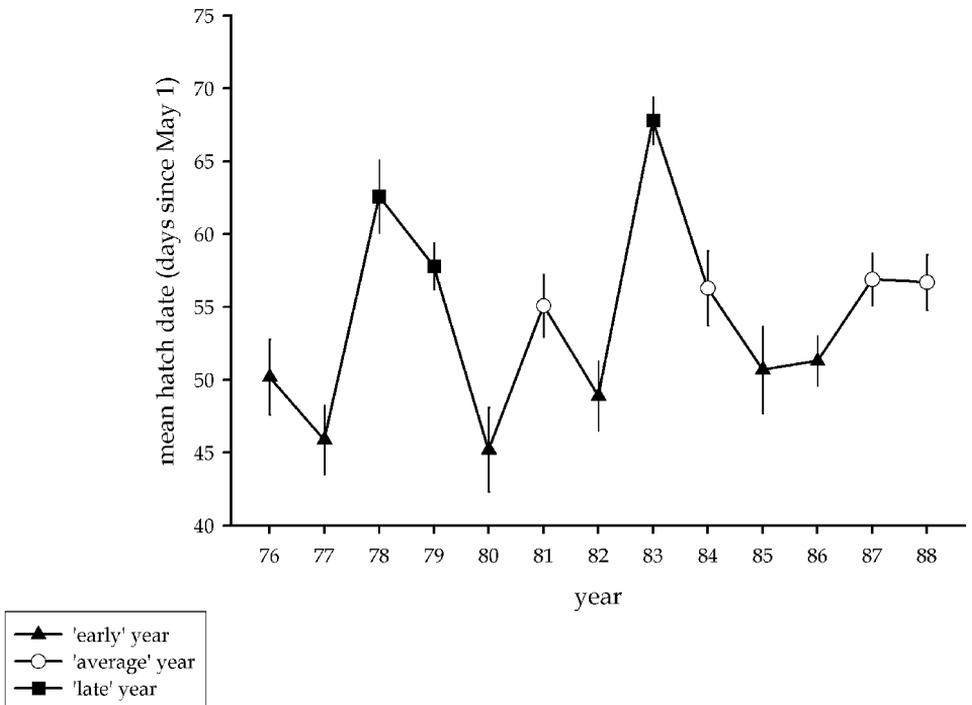

FIG. 1. Annual variation in mean hatch date (days since 1 May) of snow geese nesting at La Pérouse Bay, Manitoba, Canada. Differences in symbols reflect rankings of individual years as either 'early, 'average' or 'late'.

date $+ 0.45 \times SD$). In most years this partitioning resulted in approximately 33% of nests being classified in each of the three categories. The use of discrete categories for relative hatch dates is discussed later.

2.3 Survival estimation

Recently, Burnham (1993) derived a likelihood for separate estimation of true survival and permanent emigration rates (where permanent emigration refers to an individual leaving the sampling region permanently over the entire annual cycle; see Cooch *et al.*, 2001) using combined dead recovery and live encounter data. I used the approach described by Burnham to derive robust estimates of juvenile survival, using combined live recapture and dead recovery data for 2627 females that were banded and weighed as goslings during ringing drives at La Pérouse Bay from 1976-1988 (live encounter and dead recovery data up to and including 1990 were included in the analysis). While it is normally not possible to estimate survival rates from birds banded as young using only data from dead recoveries (Anderson *et al.*, 1985), the additional information provided by the live encounters eliminates this restriction.

In this study, the motivation for using the combined live-encounter dead-recovery approach was twofold. First, I wanted to make maximum use of all of the available data. Although the total number of dead recoveries of birds banded as goslings is low (relative to the sample of subsequent live encounters), the additional information provided by including the dead recoveries in the analysis can significantly improve the precision of the estimates of survival. Second, Cooch *et al.* (2001) showed that there were significant long-term changes in the pattern of fidelity of surviving female goslings to La Pérouse Bay, concurrent with long-term changes in environmental conditions. By combining live encounter and dead recovery data, I was able to analyse variation in survival independent of variation in fidelity to the colony.

Analyses were restricted to individual females that were (i) banded as goslings, (ii) measured at the time of banding, and (iii) for which hatch date was known. Although gosling sex is potentially a good genetic marker for growth rate (Cooke *et al.*, 1995; Cooch *et al.*, 1996, 1997), I restricted the analyses to female goslings only, for the following reasons. First, only web-tagged goslings were weighed and measured at ringing. The sample of web-tagged goslings represents a very small proportion of the total number of ringed goslings ($< 5\%$), and hence the sample of dead recoveries for this subset of the data is small. Although it is possible to supplement a recovery analysis with live encounter data (the La Pérouse Bay data set contains significantly more live encounters than dead recoveries), male goslings disperse from the breeding colony, and there are effectively no live encounters of surviving male goslings at La Pérouse Bay (Cooke *et al.*, 1995). Second, Francis & Cooke (1992) found that although survival of male goslings was significantly lower than female goslings, these differences, they argued, reflect sexual differences in dispersal. Young male snow geese choose their mates on the wintering grounds, and tend to return to the natal colony of the female (Cooke *et al.*, 1995), following migration routes with different survival and recovery rates. Since natal dispersal is a characteristic of gender, and not body size, comparison of post-fledging survival of male and female goslings is unlikely to be informative with respect to the role of body size on survival.

Encounter data consisted of (i) recoveries of dead individuals made between September and March (i.e. during the non-breeding season), and (ii) live encoun-

ters made during the breeding season at La Pérouse Bay. I maximized the sample size of 'live encounters' by combining several sources of information; an individual was classified as being 'encountered alive' if it was observed either (a) at ringing, (b) during brood rearing, or (c) on or near a nest during incubation.

2.3.1 Modelling survival: model parameterization.   In a recent study, Cooch *et al.* (2001) showed that the most parsimonious model for joint live re-encounter-dead recovery data using all females banded as goslings at La Pérouse Bay (including both measured and unmeasured individuals) had two age-classes (juvenile and adult) for survival (S), reporting (r; Seber, 1970) and fidelity (η) rates, and four age-classes for recapture rate (p, where the final age class pooled adults age 5 years and older). Cooch *et al.* (2001) found significant long-term trends in both juvenile and adult survival and recovery rates (consistent with earlier results from Francis *et al.*, 1992), and significantly declining fidelity rates for both age classes. No significant annual variation in live encounter rate was detected. In this study, I retained the age-specific and linearly constrained parameterization for reporting rates, and the constant age-specific parameterization for encounter rates for each of the models in the candidate model set (described below). Preliminary analysis showed insufficient data to achieve consistent numerical convergence using a model that constrained age-specific fidelity rates to be a linear function of time (since many of the estimates were very close to the 1.0 boundary for the adult age class). Thus, I used a 2 age-class model for fidelity, with estimates for the first age-class constrained to be a linear function of time, and constant adult fidelity. To allow for possible heterogeneity in any linear trend in fidelity rates of surviving goslings, I included full interaction among hatch periods in the general model. In the general model, adult survival was constrained to be a linear function of time. However, since I was interested in sources of annual variation in first-year survival, I adopted a time-specific parameterization for gosling survival in the general model. To test for the possible effect of the long-term environmental deterioration at La Pérouse Bay on the relationship between fledging mass and first-year survival, I also included models where first-year survival was constrained to be a linear function of time.

   The most obvious approach to analysis of variation in first year survival would be to approach the analysis using a 'full factor' design, including both body mass and hatch date as individual covariates, and absolute hatch date and year coded as classification factors, analogous to analysis of covariance (ANCOVA). However, there is significant heterogeneity in the distribution of individual body masses as a function of differences in both relative and absolute hatch date. Due to the significant seasonal decline in growth rates with increasing hatch date, there is little overlap in the distribution of age-adjusted body mass among nests hatching relatively early and relatively late within a given year (Fig. 2(a)). Thus, it is difficult to make robust inference about the relationship between size and survival, controlling for hatch date; such an analysis would, in effect, be attempting to interpolate the relationship between body mass and survival for hatch dates where data from some values of body mass are absent. For example, individuals with the smallest body masses are found only from late hatching nests—attempting to infer what the survival of these smallest individuals might be if they had hatched from an earlier hatching nest is difficult if the overlap in body mass among individuals hatching at different times is low.

   However, if body mass is expressed as a relative deviation from a mean calculated
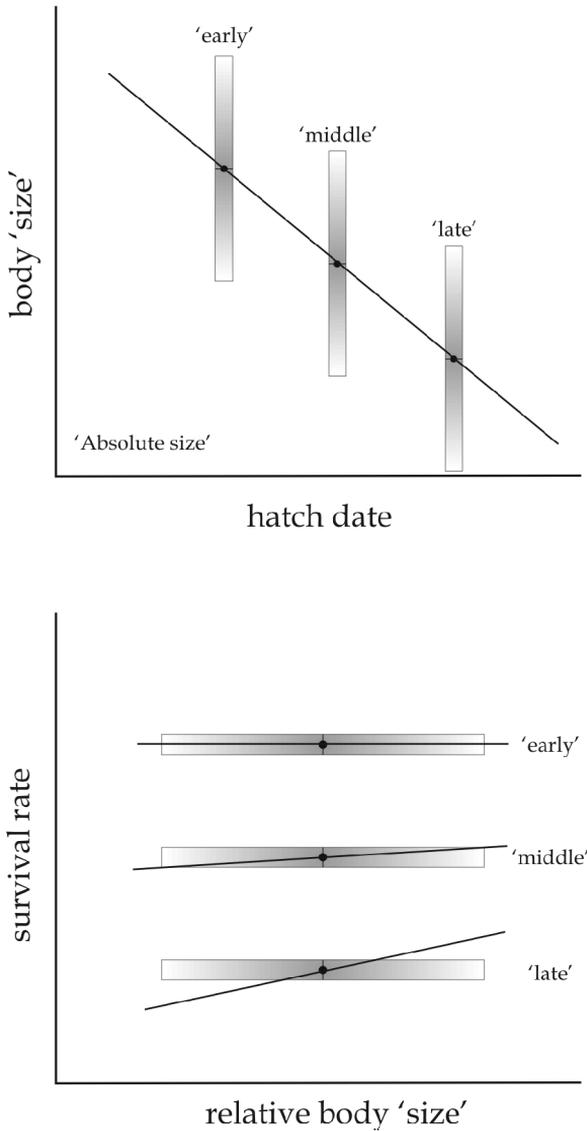
Fig. 2. Schematic outlining rationale for analysis of gosling survival as a function of relative body size. (a) Conceptual relationship between hatch date (within season) and the distribution of age-corrected gosling size at fledging. Solid line indicates overall decline in mean gosling size at fledging with increasing hatch date. Dots (•) represent mean gosling size for 'early', 'middle' and 'late' hatching goslings, respectively. Shaded bars indicate Gaussian distribution of residuals around the mean for each hatch period (greater density of shading corresponding to more data points near the mean value). (b) Conceptual relationship between age-corrected body size subsequently corrected to the mean body size within hatch period and subsequent first-year survival (see Section 2.3.1). Mean values for mean corrected body size the same (~ 0) over all hatch periods. Solid lines represent one possible scenario for the relationship between mean corrected size and survival: among early hatching goslings, there is no difference in survival among goslings of different sizes. However, with increasing hatch date, there is higher survival among relatively larger individuals, with survival decreasing with hatch date for goslings of a given size, more rapidly among relatively small goslings (interaction of survival rate with hatch period and body size).

among all birds hatching at a given time, then it is possible to analyse the effect of
'relative body size' on survival, since the mean of these 'scaled' body sizes will be
equal (~ 0) for each hatch period (Fig. 2(b)). This allows for analysis of covariance
of first-year survival with relative body mass among individuals that hatch at
different times. Of course, this raises the question of whether analysis of relative
body mass (as opposed to absolute body mass) is relevant. I believe it is, for the
following reasons. First, the primary interest of this study is the degree to which
selection may be operating on the environmental component of body mass. Previous
studies have shown that the seasonal decline in gosling growth is due to systematic
changes in the environmental component. Thus, differences in survival as a function
of variation in size for a given hatch period are likely to reflect selection on the
genetic component, since the major environmental component (hatch date) is
controlled for. Second, the differences in absolute size will be reflected in differences
among hatch periods in average survival. However, it should be noted that absolute
size at any point in time is simply the expression of the (genotype × environment)
interaction, and characterizing fitness differences using absolute size alone may not
be informative about the evolution of the trait.

Hence, I analysed the relationship between gosling body mass and first year
survival in two stages. I first analysed a set of models that included a group effect
allowing for differences in gosling survival between the three hatch date groups
('early', 'average', and 'late'; see Section 2.2). Gosling body mass, included as a
linear covariate, was scaled relative to the mean body mass for a given hatch date
grouping. Analysis of variance of these scaled values showed no significant differ-
ence in the mean among groups, and no significant heterogeneity (Levene's test)
in the variance among groups. Since the major intention of this initial analysis was
to test for heterogeneity among hatch date groups, the general model included a
(hatch group × body mass) interaction term. To control for the effects of annual
variation in absolute hatch date (Fig. 1), the general model also included absolute
hatch date coded as a second classification factor (see Section 2.2). I accounted
for the possible effects of the long-term decline in environmental conditions by
including a linear trend over years. Since I included what I believed were the two
primary sources of annual variation in gosling survival in the general model
(absolute hatch date, and the linear trend), the general model was not parameterized
to include fully time-specific differences in survival among years. The candidate
model set included the general model, plus a series of reduced parameter models
that included models where the data from the 'early' and 'average' hatch periods
were pooled, reflecting results of a preliminary analysis of live encounter data
presented by Cooke *et al.* (1995). If significant heterogeneity among hatch periods
was detected, I proceeded with a second stage of the analysis, where each hatch
period was analysed separately.

2.3.2 Modeling survival—model notation. General model notation followed
Lebreton *et al.* (1992). Since the model structure for parameters p, r and η was
held constant over all models in the model set (see above), individual models are
referenced by the model structure for the survival parameter S only. The factorial
structure of the gosling survival model is represented using 'g' for group (hatch
period) effects, 'lin' for linear time effects, and '.' for constant over time. I used g_3
to indicate three hatch periods, and g_2 to indicate the pooling of 'early' and 'middle'
into a single hatch period (Cooke *et al.*, 1995). Inclusion of gosling mass at fledging
as an individual covariate is indicated by 'w' (w^2 for the square of gosling mass).

Annual differences in absolute timing of hatch were represented as either 'abs-grp' or 'abs-lin' (entered as a classification variable or a linear covariate, respectively; see above). Only two possible models for adult survival were included in the model set: adult survival constrained to be a linear function of time ('lin'), and constant over time ('.'). Relationships among factors were indicated using standard linear models notation. Since using 'abs-grp' (categorical variable) has a greater number of degrees of freedom than using 'abs-lin' (linear covariate), the general model included 'abs-grp'. The general model for the analysis of variation in survival among hatch periods was thus S{goslings: g $\times$ lin $\times$ abs-grp $\times$ w, adults: lin}. However, as noted, GOF was assessed for the general model excluding the individual covariates (i.e. model S{goslings: g $\times$ lin $\times$ abs-grp, adults: lin}.

2.3.3 Modelling survival: model selection. Following Burnham & Anderson (1998), I first defined a candidate model set that included a general global model that (i) was sufficiently parameterized to include all of the effects believed relevant to the analysis, and (ii) reflected results from previous analysis of one or more of the individual parameters. Selection among models in the candidate model set was based on comparison of the QAICc (Lebreton *et al.*, 1992; Burnham & Anderson, 1998).

At present, there is uncertainty concerning the most appropriate approach to GOF testing methods for models including individual covariates (G. White, personal communication). Hence, I assessed the fit of the most general model without individual covariates in a given candidate model set to the data. The overall fit of this general model was assessed by comparing the observed deviance of the general model against the distribution of deviances from 100 bootstrapped data sets. The quasi-likelihood parameter was estimated by dividing the observed model $\hat{c}$ by the mean of simulated values of $\hat{c}$ from a bootstrap GOF testing of the general model (parameterized without the individual covariates relative hatch date and body size). Adjustment of the model fit using values of $\hat{c} \leqslant 3$ is generally robust (Lebreton *et al.*, 1992). Since including covariates in a model might, in fact, account for some of the lack of fit for a particular model, then the $\hat{c}$ from a model without covariates may be somewhat overly conservative. As an *ad hoc* test, I compared the relative model rankings for each model set using the bootstrapped value of $\hat{c}$ with the rankings observed if $\hat{c} = 1.0$.

Comparisons among models in the candidate set were accomplished by deriving an index of relative plausibility, using normalized Akaike weights (w_i; Burnham & Anderson, 1998). The ratio of w_i between any two models indicates the likelihood to which the model with the greatest Akaike weight is better supported by the data than the other model. The inverse of this ratio is the likelihood of a given model. To account for uncertainty in model selection in certain analyses (Burnham & Anderson, 1998), parameter estimates $\hat{\theta}$ and associated standard errors were derived by averaging over all models in the candidate model set with common elements in the parameter structure, weighted by Akaike model weights (Buckland *et al.*, 1997). All models were fit to the data using program MARK (v. 2.1; White & Burnham, 1999).

3 Results

3.1 Factorial analysis (relative hatch date as classification variable)

For the 2627 female goslings in the data set, the goodness of fit (GOF) to the

TABLE 1. Summary of analysis of variation in survival among hatch periods (see Section 2.3.1) for 2627 female Snow Goose goslings ringed at La Pérouse Bay, Manitoba, Canada (1976-88). Goslings were categorized (g_x) as 'early', 'middle' or 'late' hatching (see Section 2.3.1). Only models with QAICc weights > 0.05 are listed ($\hat{c} = 1.37$), with the most parsimonious model at the top. Model notation is described in the text (Section 2.3.2)

Model	$QAIC_c$	$\Delta QAIC_c$	$QAIC_c$ weight
$S\{gos: \text{abs-lin}, g_2 \times w, \text{adt: lin}\}$	6421.7	0.00	0.488
$S\{gos: g_2 \times \text{abs-cat} \times w, \text{adt: .}\}$	6423.0	1.31	0.254
$S\{gos: \text{abs-lin}, g_2 + w, \text{adt: lin}\}$	6423.1	1.37	0.246
$S\{gos: g_3 \times \text{abs-cat} \times w, \text{adt: lin}\}$	6425.1	3.34	0.142

general model (without the individual body mass covariate—see above) was satisfactory ($P < 0.18$). The bootstrapped estimate for $\hat{c}$ was 1.37.

The most parsimonious model for this subset of the data was one in which gosling survival was constrained to be a linear function of body mass at fledging, and absolute hatch date coded as a linear covariate, but with significant heterogeneity among hatch periods where data from 'early' and 'middle' hatch periods was pooled (model $S\{$gosling: abs-lin, $g_2 \times w$, adult: lin$\}$; Table 1). This model was almost twice as well supported by the data as the equivalent model where the relationship between survival and body mass was additive among the two hatch periods (model $S\{$gosling: abs-lin, $g_2 + w\}$). Further inspection of each of the models in the candidate model set indicated that a model including an interaction among hatch periods was better supported by the data than was a structurally similar model without the interaction in five out of six comparisons, whether or not the model included body mass as an individual covariate. Reducing the quasi-likelihood adjustment from 1.37 to 1.0 (i.e. adopting a less conservative adjustment) did not change the overall model rankings (although, clearly, the numerical values of the model AIC's changed). Given the consistency of evidence supporting a significant interaction among hatch periods, I proceeded to partition the interaction between 'early/middle' hatching and 'late' hatching goslings, by analysing each group separately.

3.2 Partitioning the interaction among hatch periods

For the analysis of each hatch period separately, the candidate model used for each period set was essentially identical to that used for the preceding analysis, with the following differences. First, since this set of analysis considered variation in survival within a hatch period, the main 'hatch period' effect and all interaction terms involving this effect were dropped. Second, although the results of the preceding analysis did not indicate support for models controlling for the long-term decline over years, I included such a constraint in the general model for within-season analyses. Finally, I also included the square of relative body mass to account for possible non-linearity in the relationship between survival and body mass. Goodness of fit (GOF) testing for the general model followed procedures used in the preceding analysis.

TABLE 2. Summary of analysis of variation in survival within hatch periods for 2627 female Snow Goose goslings ringed at La Pérouse Bay, Manitoba, Canada (1976-88). Goslings were categorized as either 'early/middle' hatching ($n = 1,689$) or 'late' hatching ($n = 938$). Models with QAICc weights > 0.05 are listed, with the most parsimonious model at the top. Model notation is described in the text (Section 2.3.2)

Model	QAIC$_c$	ΔQAIC$_c$	QAIC$_c$ weight
(a) Early/middle hatching goslings ($\hat{c} = 1.31$)			
S\{gos:., adt:.\}	5017.3	0.00	0.162
S\{gos:., adt:lin\}	5017.3	0.02	0.160
S\{gos: abs-lin, adt:.\}	5018.5	1.13	0.092
S\{gos: lin, adt:.\}	5018.6	1.28	0.085
S\{gos: lin, adt:lin\}	5019.1	1.70	0.069
S\{gos: abs-cat, adt:lin\}	5019.3	1.83	0.065
(b) Late hatching goslings ($\hat{c} = 1.44$)			
S\{gos:lin, abs-lin, w, w^2, adt:.\}	1649.9	0.00	0.183
S\{gos:lin, abs-cat*w, adt:.\}	1649.9	0.03	0.180
S\{gos:lin, abs-lin, adt:lin\}	1650.5	0.55	0.139
S\{gos:abs-lin, w, w^2, adt:.\}	1650.8	0.94	0.114
S\{gos:lin, abs-lin, w, w^2, adt:.\}	1651.1	1.20	0.100
S\{gos:lin, abs-lin, w, w^2, adt:lin\}	1651.8	1.88	0.072

3.2.1 Early/middle hatching goslings.   For the 1771 female goslings in the 'early/ middle' hatch period, the goodness of fit to the general model (without the individual body mass covariate—model S\{gosling: lin $\times$ abs-cat, adult: lin\}) was satisfactory ($P< 0.34$). $\hat{c}$ was estimated at 1.31.

Among the goslings hatching in the 'early/middle' period, there was no evidence of a relationship between gosling survival and size. The most parsimonious models were S\{gosling:., adult:.\} (i.e. constant first-year and adult survival among years) and S\{gosling:., adult: lin\} (i.e. constant first-year survival, linear trend in adult survival). Both models had approximately equal support in the data (Table 2), and were only marginally better (~ 2 times) than the next three models, which showed some support for (i) variation in first year survival as a function of absolute hatch date, and (ii) a linear trend over time in first year survival. It should be noted that differences in relative support of this magnitude are unlikely to constitute a large degree of support for the superiority of one model over the other (Royall, 1997; D. Anderson, personal communication). Moreover, as $\hat{c}$ increases > 1.0, the relative scaling of support changes in a non-linear fashion, such that differences in model support cannot be easily evaluated using 'rules of thumb' based on absolute differences in model weights. However, no model where first-year survival was constrained to be a function of body mass at fledging had any appreciable support (QAIC weights $\leqslant 0.05$), supporting the contention that there is no compelling evidence for a detectable effect of body mass on gosling survival among early hatching goslings. Using a value of $\hat{c} = 1$ did not change this general result, although there were marginal changes in the model rankings (more parameterized models increased in model weight). Averaged over all models in the candidate model set, gosling survival showed little variation over years (Fig. 3). Even though early and late years differed by as many as 30 days (Fig. 1), differences in survival among goslings hatching relatively early were extremely small ($< 2\%$).
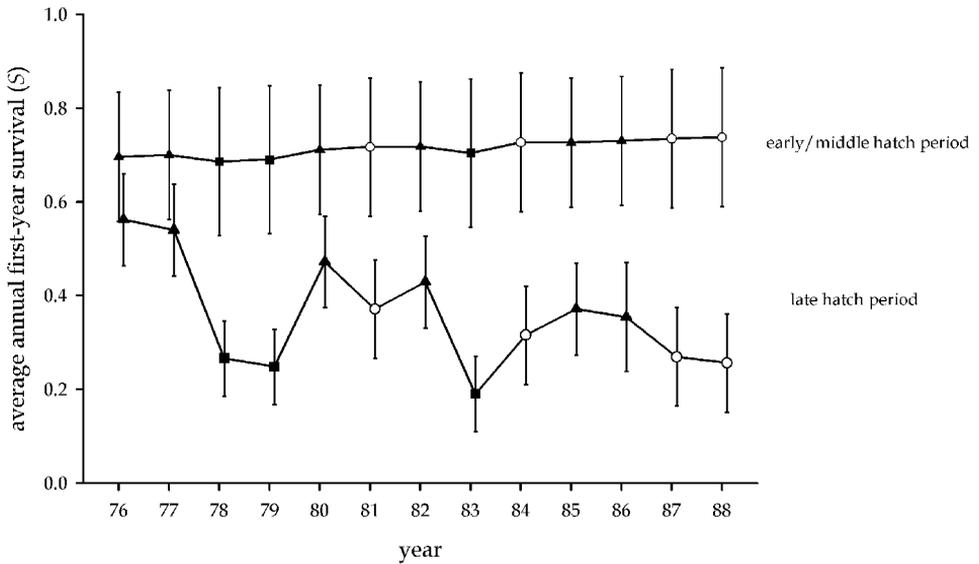
FIG. 3. Average annual survival rates for goslings ringed at La Pérouse Bay, Manitoba, Canada (1976-88), as a function of relative hatch date ('early/middle', 'late'). Values (shown with standard errors) represent estimates averaged over all structurally consistent models in the candidate model set, weighted by normalized QAICc weights for each model (see text). Symbols correspond to ranking of year as 'early', 'average' or 'late' (Fig. 1). Individual body size, adjusted for age at ringing and corrected to mean size within hatch period, was included as a covariate in some models (Table 2).

3.2.2 Late hatching goslings.   For the 856 female goslings in the 'late' hatch period, the goodness of fit (GOF) to the general model (without the individual body mass covariate—model $S\{$gosling: lin × abs-cat, adult: lin$\}$) was satisfactory ($P < 0.25$), although $\hat{c}$ was estimated at 1.44. Inspection of the data suggested that much of this lack of fit was due to sparseness of the data (approximately 1/3 of the total sample), rather than inadequacy of the model structure.

Among late hatching goslings, there appeared to be strong evidence of a relationship between gosling survival and size. The two most parsimonious models included body mass as covariates, with absolute hatch date code as a linear covariate and categorical variable (respectively), and a linear trend covariate (models $S\{$gosling: lin, abs-lin, w w^2, adult: .$\}$ and $S\{$gosling: lin, abs-cat, w, adult: .$\}$—Table 2). Support for these models was virtually equal, such that there is little support for a significant second-order effect (w^2). These models had marginally greater support in the data than the next three models, which differed primarily in the absence of the linear trend term. Only one model of the top six models (which together comprised ~80% of the total model support in the candidate model set) did not include body mass as an individual covariate. As in the preceding analysis of early/middle hatching goslings, using a value of $\hat{c} = 1$ did not change this general result. Among late-hatching goslings, first-year survival averaged over all models in the candidate model set showed marked variation over years (Fig. 3). In contrast to annual estimates from early hatching goslings, there were large differences in survival among years as a function of absolute timing, and an indication of a significant trend (decline) over time. Gosling survival differed by as much as 25% between early and late hatching years, and appeared to decline from ca. 50-60% in 1976 to 20-25% in 1988.

   Estimates of survival on the normal scale reconstituted from parameter values for model $S\{$gosling: abs-lin, w w^2, adult: .$\}$ (which was the most parsimonious model that did not include a linear trend constraint) show that survival among late-hatching goslings decreased with decreasing body mass at fledging (Fig. 4(a)), with the magnitude of the decrease being progressively larger with increasing lateness of the year. The marginal degree of non-linearity of the relationship between body size and survival evident in the data is seen by the relatively flat fitness curve among relatively larger goslings. The average survival among smaller late-hatching goslings is clearly lower than the average survival among larger late-
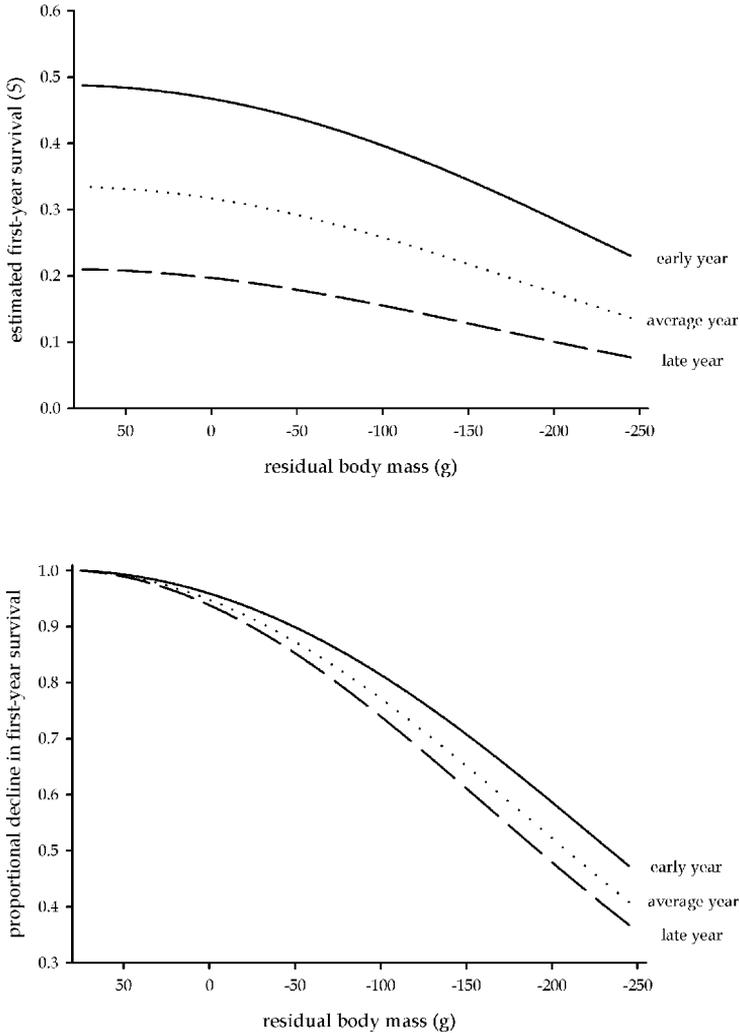
FIG. 4. Relationship between residual body mass (in g, adjusted for differences in age at ringing) and estimated first-year survival among late-hatching goslings at La Pérouse Bay, Manitoba, Canada (1976-88) on absolute (a) and proportional (b) scales, as a function of annual differences in timing of hatch (early, average, or late years). Range of residual mass values reflects range of body sizes encountered among late-hatching goslings. Values represent estimates derived from the logistic equation from the most parsimonious model not including term for linear trend over years (Table 2(b)).

hatching goslings, most notably in late years, where the difference in survival is ~25-35% (Fig. 4(b)).

4 Discussion

In a seminal paper, Cooke *et al.* (1984) showed clearly that late-hatching goslings have lower average rates of recruitment than do goslings from early hatching nests. Perhaps the most parsimonious explanation for these results is simply that late-hatching goslings do not have sufficient time to reach a critical minimum size necessary for successful migration from the colony. This simple constraint may be particularly acute for Arctic-breeding species where the short breeding season undoubtedly imposes a severe selective pressure against delayed breeding.

However, the strong interaction of gosling growth with variation in the environment suggests that this simple interpretation may be insufficient to characterize fully the pattern of selection on timing of breeding, growth rate and survival. Body size in geese has been demonstrated to be highly sensitive to even small changes in conditions experienced during early growth (Cooch *et al.*, 1991a; Sedinger & Flint, 1991; Larsson & Forslund, 1992; Lindholm *et al.*, 1994; Lepage *et al.*, 1999). Systematic changes in gosling size, both among and within years, have been shown to reflect the interaction of the underlying genetics with changes in the environmental condition experienced by goslings during early growth (Cooch *et al.*, 1991a,b; Sedinger & Flint, 1991; Larsson & Forslund, 1992; Sedinger *et al.*, 1997; Larsson *et al.*, 1998).

At La Pérouse Bay, late-hatching goslings grow more slowly (Cooch *et al.*, 1991a), and have lower overall survival and recruitment (Cooke *et al.*, 1984). Further, the long-term deterioration of the environment has been marked by a significant decline in gosling growth (Cooch *et al.*, 1991b) and survival over years (Francis *et al.*, 1992; Cooch *et al.*, 2001). While this would seem to imply that reduced size of goslings (both within and among years) leads to lower survival, interpretation of such a relationship is potentially complex. As noted by Lynch & Arnold (1988), analysis of growth components is fundamentally different from analysis of 'fixed' traits, since growth components are only expressed conditional on surviving to the point at which individuals are enumerated. Mortality during the period of study will lead to a 'selected' set of individuals, which will reduce the range of traits expressed later in life. It is conceivable that much of the mortality selection operating on body size operates prior to fledging and that, although there is significant size variation among individuals at fledging, it may be that 'only the good birds remain alive'. In fact, the probability of surviving from hatch to banding has declined over time at La Pérouse Bay (Cooch *et al.*, 1993; Williams *et al.*, 1993). If only 'good birds' remain alive at fledging, then it might be reasonable to expect that the selection gradient on body size after fledging is effectively neutral (i.e. flat), and that the observed decline in post-fledging survival reflects other factors. However, Francis *et al.* (1991) show clearly that the long-term decline in first-year survival among goslings from La Pérouse Bay does not reflect systematic variation in mortality due to hunting, but is primarily due to changes in the non-hunter component.

Even if there is clear evidence that changes in average growth and size of goslings lead to corresponding changes in first-year survival, predicting the ultimate evolutionary consequences of this relationship is conditional on the degree to which mortality operates on the environmental or genetic components of gosling size. In

this paper, I have attempted to address this question, by assessing the relationship between size and survival after controlling for major sources of variation in the environmental component of gosling growth and development—principally, timing of hatch. Analysis of variation in first-year survival indicates that, among nests hatching relatively early in a season, there is no apparent relationship of body mass and survival (Table 2). In contrast, among relatively late-hatching goslings, there was fairly strong evidence supporting a difference in survival as a function of gosling mass; smaller goslings appeared to have generally lower rates of survival, with some evidence of a non-linear relationship between size and survival (Table 2), particularly in absolutely late years (Fig. 4). Using body mass as an individual covariate clearly suggests that the magnitude of the reduction in survival with decreasing size among late-hatching goslings was directly related to the lateness of the year (Fig. 4); this interaction was not detected when size was partitioned into discrete categories (Cooke *et al.*, 1995).

4.1 *Evidence for selection—evolutionary response?*

Cooke *et al.* (1995) assumed that most of the variation in size among late hatching goslings reflects differences in the environmental component of gosling size. On average, this is undoubtedly true—the slower growth of late-hatching goslings has been shown to be unequivocally due to systematic reductions in the environmental component of growth (Cooch *et al.*, 1991a,b; Sedinger *et al.*, 1997). As such, they interpreted the lower survival of smaller late-hatching goslings as reflecting mortality due to variation of the environmental component of growth. If, in fact, mortality selection is operating exclusively on the environmental component of body size, then concluding that mortality selection on body size may be 'selectively neutral' in terms of likely evolutionary response may be reasonable.

However, there are several reasons to re-evaluate this interpretation. Clearly, the conclusion of 'selective neutrality' is likely only strictly correct if the variation in size of late-hatching goslings is entirely independent of the underlying genetics (i.e. if all of the variation in size is environmental). While the seasonal decreases in gosling growth and size at fledging are primarily environmental in origin, it is also likely that much of the variation among goslings hatching at the same time is genetic in origin. By controlling for hatch date, we are implicitly controlling for a significant source of environmental variation, such that an increased proportion of the observed variation among goslings is thus due to genetic differences among individuals. Results from an earlier analysis of variation in fledging sex-ratio at La Pérouse Bay (Cooch *et al.*, 1996, 1997) are consistent with this hypothesis. In snow geese, there is strong asymmetry in the growth of male and female goslings under different environmental conditions. Males generally grow faster and achieve larger fledging size than do female goslings, but the magnitude of this difference is smaller among late hatching goslings, implying different norms of reaction for the two 'growth genotypes' (i.e. males and females). However, there are still significant differences in size between the sexes, even among late-hatching goslings. This suggests that at least some of the variation among late hatching female goslings used in this study is likely to be genetically based, with phenotypically larger individuals also likely to be genetically larger, at least on average.

Thus, concluding that fledging size is selectively neutral may be premature, pending more precise characterization of the norm of reaction of gosling growth under different environmental conditions, something that may be difficult to do

under natural conditions in a wild population. What does appear to be clear, however, is that larger, faster growing goslings do appear to have a greater probability of survival than slower growing goslings under 'constrained' conditions, which might include (i) lack of sufficient time to reach minimum size (the increasingly lower survival of late-hatching goslings with increasingly late years; Fig. 3), and/or (ii) reduced abundance of forage. It is of note that La Pérouse Bay is located near the southern extent of the breeding range for snow geese, such that the breeding season is significantly longer than typically observed at colonies at higher latitudes, and therefore that a late year at La Pérouse Bay is relatively average for more northerly colonies. Further, differences in season length also relate to differences in overall food abundance and species composition of primary forage plants, such that foraging conditions at La Pérouse Bay (at least in the early years of the study) were superior to those typically observed at more northerly colonies. Thus, it is possible that body size is selectively neutral *at La Pérouse Bay under typical conditions*, primarily because of the lack of significant 'constraints' on growth conditions. Cooch *et al.* (1992) suggested a similar hypothesis to provide some explanation for the lack of a clear relationship between body size and other fitness characters at La Pérouse Bay as has been demonstrated at more northerly colonies. However, as the conditions at La Pérouse Bay have deteriorated in recent years, a greater proportion of goslings are unable to achieve the minimum size required for growth under increasingly 'constrained' conditions, leading to a progressive decline overall in first-year survival (Francis *et al.*, 1992; Cooch *et al.*, 2001).

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